Influence of Environmental Factors on Bacterial Biofilm Formation in the Food Industry: A Review

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Abstract
Formation and development of bacterial biofilms in the food industry could be a cause of food contamination, compromising food safety and shelf-life. Among the factors modulating biofilm formation, this review will focus in conditions normally encountered by bacteria in food environments, especially in biofilm initiation and development. The effect of environmental factors (substratum, temperature, oxygen concentration, hydrodynamic effects, food matrix composition, and microbial interactions) on biofilm formation is multifaceted and, in many circumstances, their influence could be compensatory. A better knowledge of these factors would allow for a better control of biofilm formation, either by avoiding and/or eradicating biofilms or by defining adequate Hazard Analysis and Critical Control Point systems in the food industry.

Keywords: bacterial biofilm, biofilm, environmental factors, food industry, food safety, substratum

Introduction

Biofilm is the term used to describe immobile communities of organisms (sessile cells) attached to a substratum or to each other, embedded in a matrix of extracellular polymeric substances and showing an altered phenotype in comparison with that of their planktonic (free cells) counterparts (Donlan and Costerton, 2002). Bacterial biofilms have raised special awareness within the food industry, since their individuals attach to and grow on food surfaces (such as produce or animal carcasses) or food-contact substrata (such as equipment and processing environment) (Kumar and Anand, 1998; Shi and Zhu, 2009). In addition, biofilms provide shelter to microorganisms, which show great resilience to environmental stresses and increased resistance to disinfectants and antimicrobial treatments (Hall-Stoodley et al., 2004), increasing the likelihood of survival and subsequent food contamination. For these reasons, problems associated to biofilm formation are commonplace in meat, fish, dairy, and poultry processing (Srey et al., 2013).

Biofilms can act as reservoirs of persistent, cross- and post-processing microbial contaminations in food processing environments, leading to a higher risk of foodborne diseases and reduced food shelf life (Kumar and Anand, 1998; Shi and Zhu, 2009). Control measures, namely prevention of biofilm formation or eradication of existing biofilms, are required in food industries and environments to minimize the potential risk of a widespread dissemination of pathogenic strains through consumption of contaminated food. In addition to posing a threat for food safety and shelf-life, biofilms are responsible for mechanical blockages, impedance of heat transfer processes, and increases in the corrosion rate of substratum.

Biofilm formation in the food industry, as well as in other industries, is a dynamic and cyclical process that involves several steps (Shi and Zhu, 2009): a) settlement and precipitation of organic molecules on substratum (the so-called *conditioning film*), b) attraction of bacterial cells to conditioned substratum, c) survival of bacterial cells to cleaning and sanitation treatments, d) growth of surviving population

and genetic regulation (such as *quorum sensing*) to increase biofilm mass. As a last step in biofilm's life cycle, a dispersion of cells into the surrounding environment could occur (Costerton et al., 1995). It is the mechanisms behind the attachment which ultimately determine the adhesive and cohesive properties of a biofilm. Planktonic cells contact the conditioned substratum either by physical forces (such as Brownian motion or gravitational forces) or by bacterial appendages (such as flagella). Bacterial adhesion will be mediated by short-range interactions, including van der Waals forces, covalent bonds; and hydrogen, steric, dipole-dipole, ion-dipole, ion-ion, electrostatic, and hydrophobic interactions. Net interaction between a cell and the substratum has been described as a balance between two additive factors, van der Waals interactions (attractive) and repulsion interactions from the overlap between the electrical double layer of the cell and the substratum (repulsive due to negative charges of the cells). Physical appendages of bacteria (flagella, fimbriae and pili) overcome the physical repulsive forces of the electrical double layer and consolidate the bacteria-substratum association (Garrett et al., 2008).

Factors modifying the regulation of the process of biofilm formation could be classified in environmental conditions (temperature, substratum properties, nutrient availability, pH, water activity, stressing agents, etc.) and microbial characteristics (strain, cell surface, growth phase, metabolic activity, etc.). A good overview of the influence of these factors on biofilm dispersion and biofilm surveys and studies in the food industry can be found in recent review articles discussing biofilm removal strategies (Bridier et al., 2015; Karatan and Watnick, 2009; Srey et al., 2013; Van Houdt and Michiels, 2010). Therefore, this review will focus in the environmental conditions influencing biofilm initiation and development in the food industry.

Environmental factors influencing biofilm formation in the food industry

It is well known that surrounding conditions under which bacteria grow and develop can largely influence behavior of planktonic cells: growth, resistance, toxin production, etc. Among these factors, we could find temperature, nutrients, metals, osmolytes, water activity, pH, redox potential, microbial communities, interaction with host, stresses, antimicrobials, etc.

Likewise, environmental conditions can modify physiological state of cells in a bacterial biofilm. Since biofilm formation requires an interaction between bacterial cells and substratum, environmental factors can influence both bacterial properties (mediated by changes in gene regulation and/or physicochemical properties of the cell surface) and substratum properties (mainly through physicochemical changes). Next, the effect of main environmental conditions occurred in food processing on bacterial biofilm formation is described. In addition, Table 1 summarizes the general effect of these factors on biofilm formation.

Chemical composition of substratum

Among the materials used for food contact surfaces we could highlight stainless steel, glass, rubber, polycarbonate, polyurethane(Chia et al., 2009), polystyrene, polypropylene, Teflon, nitrile rubber (also known as NBR or Buna-n), titanium, aluminum, ceramic, and wood for developing countries. Generally, biofilms can develop in the surface of any of these materials (Donlan and Costerton, 2002; Hamadi et al., 2005; Simoes et al., 2010; Vazquez-Sanchez et al., 2013). The adhesion to the substratum is dependent on the physicochemical properties of the substratum such as texture (rough or smooth), hydrophobicity, and surface charge (Donlan, 2002). In turn, these factors could be modified by other environmental conditions, such as pH, temperature, and nutrient composition of the food matrix (Gerstel and Romling, 2001; Nilsson et al., 2011), as described in the following sections.

On the one hand, the most frequent material in food processing equipment is stainless steel, particularly austenitic grades 304 and 316, because of its mechanical strength, and its resistance to cleaning agents and corrosion (Pimentel et al., 2014). However, cracks and scratches caused by mechanical cleaning could allow attachment of organic residues and bacteria (Wirtanen et al., 1996). On the other hand, porosity and absorbency of wood material (frequently used in developing countries) allows for entrapment of organic material and bacteria, enhancing biofilm formation in its surface (Mariani et al., 2011).

Bacteria with hydrophobic properties tend to adhere to hydrophobic material surfaces, while those with hydrophilic characteristics would prefer hydrophilic surfaces. In addition, hydrophobic bacteria are more likely to attach to surfaces than hydrophilic bacteria (An and Friedman, 1998; Katsikogianni and Missirlis, 2004). Thus hydrophobic materials, such as plastics, are more likely to promote bacteria attachment than hydrophilic glass or metals.

Bacteria can also adhere to biotic (living) surfaces, such as vegetable and animal tissues. Microorganisms preferentially attach to intact surfaces of produce, such as roots of radish sprouts, melon surface or alfalfa sprout tissue. Likewise, *Salmonella* spp. and *Campylobacter* spp. are biofilm-forming pathogens commonly isolated from poultry meat, which could be transferred to food contact surfaces. Many types of fish-contaminated-bacteria are found to be biofilm-forming, including *Vibrio cholerae*, *V. parahaemolyticus*, *V. vulnificus*, and *V. alginolyticus* which could contaminate processing equipment in fish industry during loading, conveying, weighing, and packaging.

Actually, the slicing materials used in processing were speculated to be the source of contamination due to biofilm formation (Srey et al., 2013). Indeed, a survey of refrigerated ready-to-eat foods revealed smoked fish as the most common pathogen-contaminated food among the analyzed samples. Despite of the importance of biofilms in the surface of these food products, a few studies evaluate this biofilm formation and its control in real food surfaces, probably due to the heterogeneity of these surfaces in the same batch and reproducibility among different batches. More attention should be paid to develop of model food surfaces as a next step for food preservation.

Temperature

Temperatures in food industry could vary enormously: -18ºC in freezers, 4ºC in refrigerators, from 4ºC to 15ºC in processing plant environments, 37ºC in recently slaughtered animals, 72ºC in milk pasteurizers, and temperatures over 100ºC in sterilizers and during pipes disinfection.

Temperature can influence cell physiological state, physical properties of the compounds within and surrounding the cells (including biofilm constituents), and properties of the substratum. The matrix formed by extracellular polymeric substances (EPS) reacts to stress by exhibiting elastic tension, viscous damping, and alignment of the polymers in the shear direction. Properties of EPS, such as the viscosity of the polysaccharides, are affected by temperature: increases in the temperature of polysaccharides can lead to formation of a gel-like substance which gradually increases in strength until a critical point is reached when the gel forms a solution (Villain-Simonnet et al., 2000). Many microbial polysaccharides undergo transition from an ordered state at lower temperatures and in the presence of ions, to a disordered state at elevated temperature under low ionic environments. Consequently, the more uniform properties of polysaccharides at lower temperatures could stimulate biofilm formation (Garrett et al., 2008). Moreover, since temperature modifies solubility of food components, changes in temperature could lead to precipitation of compounds which would form the conditioning film.

In addition, incubation temperature modifies cell physiology. An optimum temperature bacterial growth rate exists for each strain: temperatures away from the optimum decrease bacterial growth efficiency. At temperatures much higher than optimum, microbial viability is also

compromised. Since nutrient metabolism is dependent on the presence and activity of enzymes, an increase in nutrient intake results in a rapid biofilm formation (Garrett et al., 2008). Incubation temperature may also affect cell surface properties, such as charge, hydrophobicity, and electron donor and acceptor characteristics (Briandet et al., 1999). For example, in *Staphylococcus aureus* and *Listeria monocytogenes*, cell surface hydrophobicity level increases with temperature, leading to a higher biofilm formation (Chavant et al., 2002; Di Ciccio et al., 2015). Additionally, temperature could change microbial transcriptomic profile: flagellin is generally repressed at temperatures above 30 °C in *L. monocytogenes* (Way et al., 2004). Although flagellum can mediate attachment, *L. monocytogenes* can also stick to substrata through a passive process independent of flagella at temperatures above 30 °C. In contrast to *L. monocytogenes* clinical strains which produce more biofilm mass at higher temperatures, isolates from food factories increase biofilm formation when temperatures decrease to 10 °C.

Although temperature modulates bacterial growth, it is considered that the effect of temperature on biofilm formation is independent of the rate of planktonic growth (Nilsson et al., 2011). Therefore, it is agreed that influence of incubation temperature on biofilm formation occurs through changes in bacterial cells rather than in substratum (Cerca and Jefferson, 2008; Nilsson et al., 2011).

Oxygen concentration

Microorganisms live in a world driven by the diffusion of molecules in aqueous environments: they are associated with host tissues, attached to inanimate objects in hydrated biofilms, or free-living in aquatic environments. As a result, these microorganisms experience the amount of O_2 that diffuses into their immediate environment (Morris and Schmidt, 2013). Moreover, mature biofilms contain concentration gradients of nutrients and metabolic products, being oxygen the best studied and most familiar example. Oxygen serves as the terminal electron acceptor for the electron-transport chain in aerobic respiration (Willey et al., 2011). In the absence of O_2 a microorganism often uses an oxidized endogenous organic molecule as an electron acceptor to reoxidize the NADH formed during glycolysis (fermentation). However, the amount of energy obtained by aerobic respiration is higher than by fermentation (Willey et al., 2011). Therefore, oxygen availability determines bacterial energy production, with a potential impact in biofilm formation. Creation of microenvironments within biofilms, such as reduced oxygen zones or restricted nutrient diffusion through biofilm, leads to slow growth of the bacteria. Decrease of oxygen and nutrient within biofilms consequently results in a decrease in bacterial metabolic activity and cessation of bacterial growth (Anderson and O'Toole, 2008). This state may not provide sufficient energy to maintain cell attachment and, consequently, trigger detachment. For example, anaerobiosis inhibits biofilm development by *S. aureus*. However, oxygen negatively regulates biofilm development by *Staphylococcus epidermidis* via activity of *sigB*. Under anaerobic conditions, a higher *sigB* expression activates *icaADBC*, leading to production of enzymes responsible for polysaccharide intercellular adhesin synthesis in *S. epidermidis* (Cotter et al., 2009).

Oxygen concentration is also involved in regulating curli expression in *Escherichia coli* through a network of interactions between transcription factors and the *csg* regulatory region. Curli or thin aggregative fimbriae promote biofilm formation to abiotic surfaces both by facilitating initial cell-substratum interactions and subsequent cell-cell interactions (Beloin et al., 2008).

In addition, oxygen also affects the surface hydrophobicity, which determines the hydrophobic interaction. In general, an increase in the surface oxygen brings about a decrease in its hydrophobicity (Moreno-Castilla, 2004).

Hydrodynamic effects: static and flow conditions

In the food industry, both static (e.g. a processing table or knife) and flow conditions

(e.g. pipes or corrugated tubing) can be found. Physical properties of biofilms, such as cell density and strength of attachment, can be affected by fluid shear: static or low flow conditions may lead to isotropic structures, but higher unidirectional flow may produce filamentous cells or groupings of cells with evidence of directionality (Goller and Romeo, 2008). However, remodeling of *E. coli* biofilms was caused by a cell biological response to shear stress rather than by a direct physical effect on the material organization itself (Galy et al., 2012).

It is generally considered that higher shear rates result in higher detachment forces leading to a decrease in the number of attached bacteria, while they make the biofilm denser and thinner (Katsikogianni and Missirlis, 2004). Although role of hydrodynamics in biofilm development and structure is of great importance, the molecular response to fluid flow is still to be elucidated. For example, growth under high shear forces induced a stronger attachment of *Pseudomonas aeruginosa* than under lower shear forces, probably because turbulent flow could impinge cells on the substratum, enhancing bacterial adhesion (Stoodley et al., 2002). However, weak rolling adhesion at low shear force allows for cells to spread out and colonize more substratum area than under high shear stress, where cells remain in tight microcolonies. Optimum flow rate is needed for bacterial attachment reflecting the balance between rate of bacterial delivery and the force acting on attached bacterium (Katsikogianni and Missirlis, 2004). As a consequence a flow that allows a stable interaction between bacteria and substrata would determine preferred sites of colonization (Goller and Romeo, 2008).

Food matrix composition

In food-processing environments, bacterial attachment is additionally affected by food matrix constituents (Van Houdt and Michiels, 2010). Biofilm formation by *L. monocytogenes* in stainless steel, conveyor belt rubber, and wall and floor materials was reduced initially by residues from meat products, but at later stages, biofilm cell counts and their resistance increased (Somers and Wong, 2004). Furthermore, biofilm formation by *L. monocytogenes* was enhanced in nutrient-poor medium rather than in nutrient-rich medium (Kadam et al., 2013).

Moreover, environmental glucose and catabolite repression inhibit multilayer biofilm formation in a variety of pathogenic and laboratory strains of *E. coli*, a number of clinical isolates of Enterobacteriaceae, and *Bacillus subtilis* (Karatan and Watnick, 2009). However, *B. subtilis* biofilm formation is activated when glucose is present at low concentrations but inhibited at high concentrations. Low glucose concentrations stimulate Spo0A in *B. subtilis*, a positive regulator of biofilm formation; and high concentrations stimulate CcpA which represses a gene that either decreases the rate of attachment of cells to a biofilm or increases the rate of detachment of cells from the biofilm (Stanley et al., 2003).

In many cases, high osmolarity of food matrix inhibits biofilm formation, although this effect may depend on the type of osmolyte. Thus, 100 mM NaCl in growth medium repressed transcription of curli genes by the transcription factor CpxR (Jubelin et al., 2005). In contrast, addition of similar concentrations of sucrose does not produce the same effect, suggesting that environmental signal is ionic strength rather than osmolarity.

Ionic strength controls the electrostatic interactions which could be either attractive or repulsive. At neutral pH both the bacterial cells and the substratum surface are negatively charged. Therefore, under these conditions, two opposite types of interactions exist: electrostatic repulsive interaction and van der Waals attractive interaction. Whether or not bacterial cells attach to a surface depends on which interaction dominates (Morisaki and Tabuchi, 2009). Increasing the ionic strength of the food matrix could reduce electrostatic interactions due to the screening effect of the surface charge produced by the added salt (Moreno-Castilla, 2004). Therefore, when the electrostatic interaction between the substratum and the cell is repulsive an increase in ionic strength will increase the attachment. Conversely, when the

electrostatic interactions are attractive, an increase of the ionic strength diminishes the adsorption. Morisaki and Tabuchi (2009) found that the rate of attachment for all the tested bacterial cells to the glass surface increased with increasing ionic strength and, at a certain level, it became steady. Increases in attachment rate might be due to the decrease in the energy barrier between the bacterial cells and the glass surface caused by ionic strength.

With regard to pH, growth in acid or alkaline conditions could modify, among others, both physicochemical properties of cell envelopes and bacterial gene expression which impact in bacterial adhesion. Chagnot et al. (2013) showed that maximal adhesion of *E. coli* O157:H7 to muscle proteins occurred at pH 7 while no significant specific bacterial adhesion could be observed at pH 5.5. Similarly, Tresse et al. (2006) demonstrated that adhesion capability of *L. monocytogenes* strains was more reduced at pH 5 than at pH 7. Decrease in adhesion of *L. monocytogenes* was correlated with a less hydrophobic cell surface, and down-regulation of the flagellin synthesis. However, biofilm formation by *Salmonella* Enteritidis in stainless steel at seventh day of incubation was found to be independent of the pH value in the range 4.5-7.4 (Giaouris et al., 2005). Besides, pH and ionic strength of the food matrix influence the bacterial surface hydrophobicity (CSH). CSH decreased at higher pH (7.4) and low ionic strength (0.5 M), while it increased at pH 2.2 and ionic strength 1 M. Consequently, bacterial adhesion to hydrophobic surfaces increased at pH between 2.2 and 4, in the range of the isoelectric point when bacteria are uncharged, and ionic strength 1 M (Katsikogianni and Missirlis, 2004). In addition, variations in pH lead to dissociation or protonation of the electrolytes, modulating electrostatic interactions between substratum and bacteria through changes in their surface charge.

Furthermore, food composition and concentration also determines formation of conditioning film in substratum which provides anchorage and nutrients to the bacterial community. Thus, the substratum could be covered by a film of organic molecules such as proteins from milk, pork, beef and even extracellular polymeric substances produced by bacteria (Shi and Zhu, 2009).

Therefore, properties of food matrix influence bacterial adhesion mostly by changing surface characteristics of both the bacteria and the materials (hydrophobicity-charge) (Katsikogianni and Missirlis, 2004). In addition, composition and concentration of food matrix could cause changes in bacterial physiology related to surface attachment.

Microbial interactions

Along with the abiotic environmental factors described above, biotic factors may also influence biofilm formation, such as interactions between different microbial populations. Coexistence of two or more bacterial species could greatly impact initiation and development of bacterial biofilms. A wide variety of bacterial species are present in food processing environments and known to form biofilms on substrata, as explained above. Therefore, complex associations of different species are established, creating an intricate and dynamic network for biofilm formation. In particular, multispecies biofilms appear to be more resistant to antimicrobials than their mono-species counterparts (Bridier et al., 2015). This enhanced resistance was linked to the protection offered by resistant species to the whole community, rather than selection for the resistant species. In addition to protection, association of strains could lead to an increase in biomass production and pathogen persistence.

However, relationship between communities is not always beneficial for all partners. In most cases, presence of a bacterial species could inhibit biofilm formation. For example, presence of *Staphylococcus xylosus* and *Pseudomonas fragi*, or bacteriocin-producing *Lactococcus lactis* reduced biofilm formation by *L. monocytogenes* (Van Houdt and Michiels, 2010).

Table 1. Main effects of environmental factors on bacterial biofilm formation in the food industry. More details and exceptions are provided in the main text.

Factor		General effect	References
Chemical composition of substratum	**Texture**	Rough surface of substratum favors biofilm initiation	(Mariani et al., 2011; Wirtanen et al., 1996)
	Hydrophobicity	Hydrophobic material surfaces favor attachment of bacteria with hydrophobic properties	(An and Friedman, 1998; Katsikogianni and Missirlis, 2004)
	Surface charge	Opposite surface charges of substratum and cell favor attachment	(Morisaki and Tabuchi, 2009)
Temperature		a) Lower temperatures lead to more uniform properties of polysaccharides, which stimulate biofilm formation b) Lower temperatures decrease cell surface hydrophobicity level, leading to a lower biofilm formation	(Chavant et al., 2002; Di Ciccio et al., 2015; Garrett et al., 2008)
Oxygen concentration		Decrease of oxygen within biofilms reduces bacterial metabolic activity and inhibits bacterial growth	(Anderson and O'Toole, 2008)
Hydrodynamic effects		Higher shear rates decrease bacterial attachment bacteria, but increase density and thinness of biofilms	(Katsikogianni and Missirlis, 2004)
Food matrix composition		a) High osmolarity of food matrix inhibits biofilm formation b) Influence of pH and ionic strength on biofilm formation through changes in surface hydrophobicity and charge	(Jubelin et al., 2005; Katsikogianni and Missirlis, 2004)
Microbial interactions		Variable effect	(Bridier et al., 2015; Van Houdt and Michiels, 2010)

Conclusions

Although influence of environmental conditions on bacterial behavior has been largely studied on planktonic cells, more information about how these factors modulate biofilm formation is required. However, we believe this is an intricate and difficult task for several reasons: adhesion of bacterial cells to surfaces and development of biofilms are highly complex processes since they are multi-factorial and compensatory. For example, changes in incubation temperature potentially modify bacterial gene expression, physicochemical properties of cell surface, pH and osmolarity of food-matrix, solubility and precipitation of nutrients, substratum properties, and even microbial interactions by favoring growth and/or survival of some communities

over the other(s), with unpredictable consequences for biofilm formation. There are multiple modes of regulating biofilm initiation via environmental factors, e.g. by a specific stress such as acid or alkaline growth conditions, low temperature (e.g. flagella-mediated attachment and biofilm initiation), and high temperature (e.g. reduced motility, passive attachment processes, altered cell surface), and each is favored based on the environmental conditions that optimally induce this response in a given strain (Nilsson et al., 2011).

In addition sessile bacteria experience multiple micro-environments depending on their location in the spatial structure of the biofilm (Bridier et al., 2015). This chemical heterogeneity leads to bacterial adaptation to their direct local micro-environment and to the emergence of a physiological heterogeneity within the biofilm, such as mechanical cohesiveness or tolerance to antimicrobial challenges and resilience to changing environmental conditions. Similarly, slow growth of cells within the biofilm due to oxygen limitation could result in subsequent bacterial recalcitrance to antibiotic treatment growth (Anderson and O'Toole, 2008).

In brief, prediction of biofilm formation and development involves many variables and factors to take into account, summarized in Table 1. A strict control and description of all these variables, including the environmental factors shown in this review, becomes necessary to future development of mathematical models for biofilm formation based on integrated data obtained by different researchers (*big data*). These models would predict biofilm formation and development according to environmental conditions and microbial characteristics. Such predictions will allow for better Hazard Analysis and Critical Control Point systems in the food industry to control problems related to bacterial biofilms. Moreover, control of environmental factors could also be a valuable tool to avoid biofilm formation and to reduce or eradicate formed biofilms. A better knowledge of these factors would allow for a better control of biofilm formation in the food industry.

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